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NUPTIAL FEEDING IN *SEPEDON* SPP. (DIPTERA: SCIOMYZIDAE)

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Abstract.—Courting males of *Sepedon fuscipennis fuscipennis* Loew, *S. f. floridensis* Steyskal, and *S. aenescens* Wiedemann release a nearly clear liquid anally that the females feed on during copulation. Other observers have indicated that an opaque, semi-solid nuptial food is secreted orally by males of *S. aenescens*, *S. senex* Wiedemann, *S. plumbella* Wiedemann, and *S. ferruginosa* Wiedemann. Males of *S. f. fuscipennis* also attract and nourish potential mates with foods (e.g. dead snails) that they discover and defend, and some *Sepedon* males mate without offering females anything. These systems are compared with other insect mating systems in order to suggest fruitful avenues for future research.

Reports in the literature suggest that mating in most species of Sciomyzidae (Diptera: Acalyptratae) is simple and direct. Published observations on a number of species in the genera *Antichaeta*, *Dictya*, *Elgiva*, *Perilimnia*, *Pherbellia*, *Shannonia*, and *Tetanocera* (see papers cited by Berg and Knutson, 1978, p. 240) all indicate that the males exhibit no distinctive courtship behavior. They simply leap onto females and quickly establish genitalic contact.

Neff and Berg (1966) observed that premating behavior in some species of *Sepedon* is far more elaborate than that indicated above. We have confirmed and extended their observations by studying one species that they also studied and two taxa not included in their report. In all three taxa, the male liberates an almost clear liquid anally that the female feeds on during copulation.

Our observations and those of others indicate that the use of attractive and/or nutritive substances, secreted anally or orally by the male, may be widespread in *Sepedon* and related genera. They also suggest differences in sites of origin of the nuptial food, and in nuptial uses of foods other than secretions, and indicate that matings sometimes occur without any food being transferred.

This paper is written to present our observations on the sequence of premating acts of *Sepedon fuscipennis fuscipennis* Loew, *S. f. floridensis* Steyskal, and *S. aenescens* Wiedemann, to enter some contrasting observations of others into the published record, to discuss and try to explain the obvious diversity and puzzling paradoxes reported, and to note the remarkable convergence in mating systems between *Sepedon* and *Panorpa* scorpionflies.

COURTSHIP OF *SEPEDON FUSCIPENNIS FLORIDENSIS*

Although described as a subspecies (Steyskal, 1951), *S. f. floridensis* is easily distinguished from *S. f. fuscipennis*, and it probably should be recognized as a

distinct species. Our observations of the courtship of this little-known taxon are based on a rearing of flies collected at Highlands Hammock State Park, Highlands County, Florida.

The essential steps in the premating sequence of *S. f. floridensis* are illustrated in Figs. 1–6. Photographic prints were made from a strip of motion picture film of a pair that mated while standing on the side of a glass breeding jar. However, resolution was lost when selected frames of this 16-mm color motion picture film were greatly enlarged and reproduced in black and white. Therefore, the prints were traced, and obscured details were filled in by studying the original color frames on the stage of a dissecting microscope. The motion picture sequence was taken through the glass, so all pictures are ventral views.

The male initiated precopulatory behavior by touching the substrate with the tip of his abdomen and depositing a droplet of clear, transparent fluid (Fig. 1). This colorless droplet, presumably expelled through the anus, can easily be overlooked. It shows well on our film only because a floodlight was positioned so that the droplet reflected its light into the camera lens.

The male then lifted the tip of his abdomen, extended his wings laterally at right angles to his body axis, and vibrated them rapidly for a few seconds (Fig. 2). His wings were then returned to their resting position over his abdomen, but he repeated the wing vibration movement several times before a female was attracted. During this time, his abdomen bobbed up and down conspicuously, and his forelegs were frequently raised, waved about, and lowered.

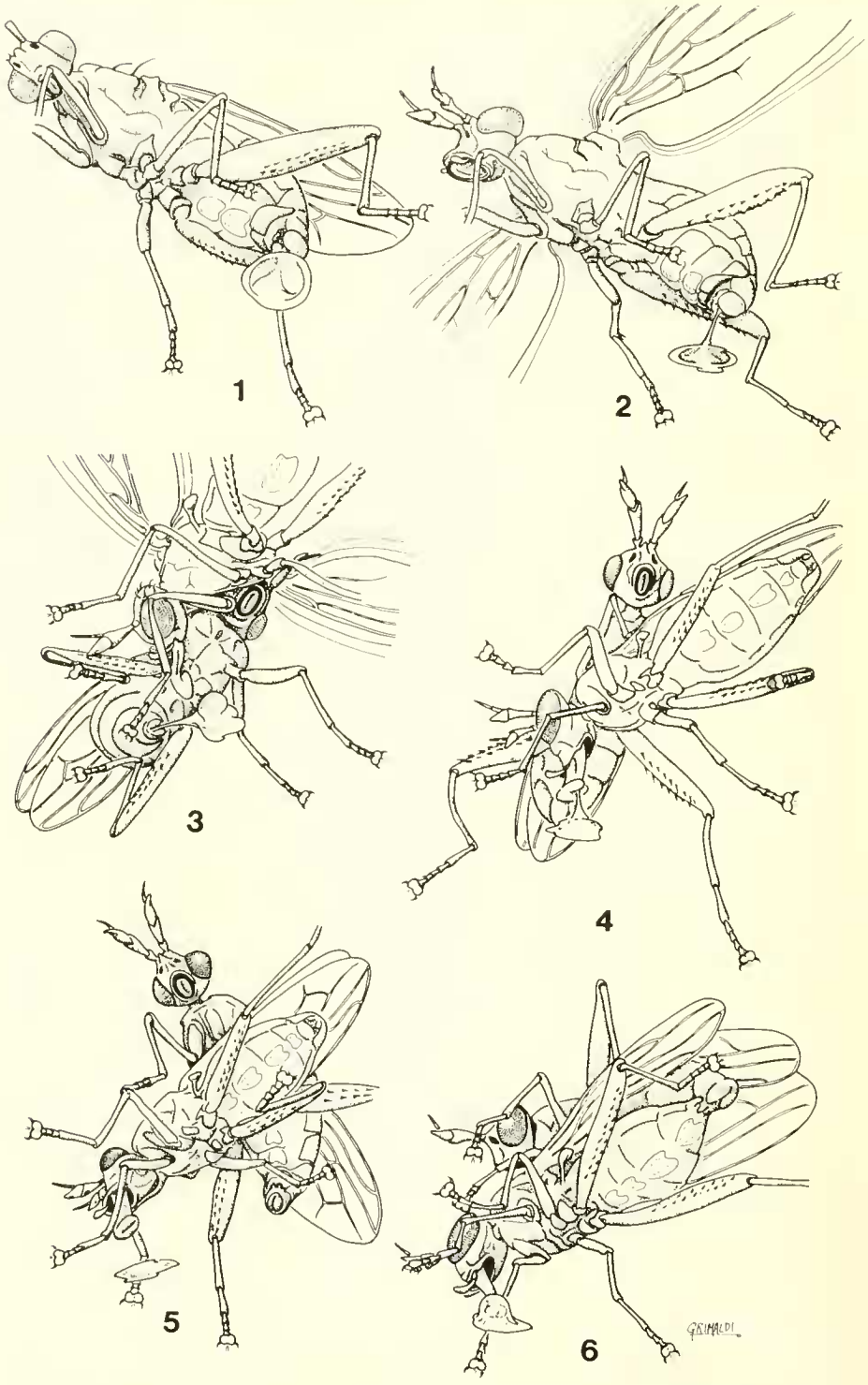
At this point in the sequence illustrated, the male noticed a female approaching from the upper right. He quickly shifted his position, facing her and placing himself between her and the droplet, so that she would have to crawl under him to reach it. The female approached in a crouching posture, with her labellum extended. For brief intervals, her wings were extended laterally and vibrated rapidly, apparently responding to the signal of the male (Fig. 3).

When the female started to feed, the male stepped onto her. They were still facing in opposite directions (Fig. 4). He rotated his body to align himself for copulation, temporarily distracting her from feeding (Fig. 5). When he attained the proper position, genitalic contact was quickly established. The female resumed feeding and continued to feed as long as copulation continued (Fig. 6).

Other matings of *S. f. floridensis* have followed the general pattern outlined above. In all instances that we have witnessed, the males have released the nuptial food anally, permitted the females to reach it only by crawling under them, mounted as they did so, and rotated their bodies to align themselves for copulation after mounting. We have never seen them whip the nuptial food into a froth with their mouthparts, as males of *S. aenescens* characteristically do, nor utilize other foods to attract females, as males of *S. f. fuscipennis* often do.

Courtship of *Sepedon fuscipennis fuscipennis*

Sepedon f. fuscipennis has been studied intensively since it was involved in the discovery that sciomyzid larvae are predatory on snails (Berg, 1953). It is therefore better known biologically than any other taxon of Sciomyzidae (see papers by Arnold, Barnes, Eckblad, Eckblad and Berg, and Neff and Berg (1966) cited by Berg and Knutson (1978); and the recent study of sciomyzid phenology (Berg et al., 1982)). Our observations of its premating behavior are based on a laboratory



Figs. 1–6. Steps in the premating sequence of *S. f. floridensis*. (See text for full explanation.)

rearing started with flies collected in Tilden Township, Berks County, Pennsylvania.

This behavior is similar to that of *S. f. floridensis* in the anally deposited liquid that is fed upon by the female during copulation and in actions of the wings, abdomen, and forelegs of the male while trying to attract her to it. It differs from *S. f. floridensis* in the direction of approach when the male mounts the female, and the use of foods other than their own secretions to attract females may also be different. Instead of interposing himself between the droplet and the female so that she must crawl under him to reach it, the male of *S. f. fuscipennis* usually leans or steps back to give her free access to the droplet. Then, after she has started to feed, he walks around behind her and mounts, already properly aligned for copulation.

Males of this sub-species sometimes utilize other foods to attract a female and keep her occupied during copulation. Our breeding and oviposition jars are routinely supplied with a small pellet of a honey-yeast mixture and a freshly killed snail for supplementary protein. If a male is the first to find either of these foods, he may frequently interrupt his feeding on it to bob his abdomen up and down, raise and wave his forelegs, and rapidly vibrate his extended wings. He permits the attracted females that give the proper wing signal to approach and feed. Then they mate and usually remain in copula as long as she continues to feed.

Whether standing guard over droplets they have produced or food materials they have discovered, males prevent other males and often prevent females from reaching the food by raising their forelegs in a threatening pose and, if necessary, charging toward them. Females apparently are permitted to reach the food material only if they vibrate their wings to signal their willingness to mate. We have not seen this signal every time we have witnessed copulation, but it is given briefly and can easily be overlooked.

This affirmative or submissive signal must be distinguished from another wing signal that has almost the opposite meaning. If a fly flicks her wings several times in quick, lateral, scissors-like movements, other flies of both sexes take this as a warning not to come any closer. This signal is especially characteristic of females that have found a food mass and are already feeding on it. However, it may help them to defend choice oviposition sites as well as food resources.

Feeding of the female during copulation is so commonly observed in *S. f. fuscipennis* that it almost appears prerequisite to mating. We have watched many matings that continued for 9 to 21 minutes in which the females fed almost continuously throughout the process. There were only a few interruptions of less than 5 seconds to groom their mouthparts. When such prolonged matings occurred on a freshly killed snail or a fresh honey-yeast pellet, the female carried the male around freely and fed over the entire surface of the food mass. A male that managed to mate 11 times in about 50 minutes accomplished this by remaining on a freshly killed snail most of that time.

Whenever the female abandoned her food source, mating was promptly terminated. The male appeared to raise up as if signalled to do so, and the female walked out from beneath him. This orderly behavior was in contrast to what we commonly observed in *Dictya* spp. (Valley and Berg, 1977), where females had to dislodge males by shaking their bodies vigorously.

The great frequency of matings in the first few minutes after flies are introduced into new breeding jars—a phenomenon that mystified us for years—also is explained by the requirement of supplying the females with acceptable nuptial food. In jars more than a day old, impenetrable crusts form over the dead snails. The honey-yeast pellets also tend to dry and harden. In new breeding jars, both types of food are moist, soft, and readily accessible. Males who find them have more than enough food and excellent opportunities to mate.

Males were never observed to produce their nuptial fluid in new breeding jars, nor to place it on freshly killed snails or honey-yeast pellets, but they frequently deposited it on crushed snails that were old and dry. Females attracted to such dried snail remains fed only in the area moistened by the droplet.

Courtship of *Sepedon aenescens*

Sepedon aenescens was introduced into Hawaii from Japan several years ago to aid in a program of biological control of the snail host of the giant liver fluke of cattle. Harry Nakao, then State Entomologist of Hawaii, kindly sent us 30 puparia of this species. The 12 pairs of adult flies (plus three extra males) obtained from these puparia afforded many opportunities to observe courtship, mating, and oviposition.

Eight days after the first flies emerged, we discovered two pairs in copula. One of the females was eating from a frothy mass of opaque, white material that was fully as large as her head (cf. Fig. 7), stuck on the side of the plastic observation cell. She seemed to pull hard every time she leaned back to tear off more material. After ingesting that, she leaned forward again to get another portion. She continued to feed throughout the process of copulation.

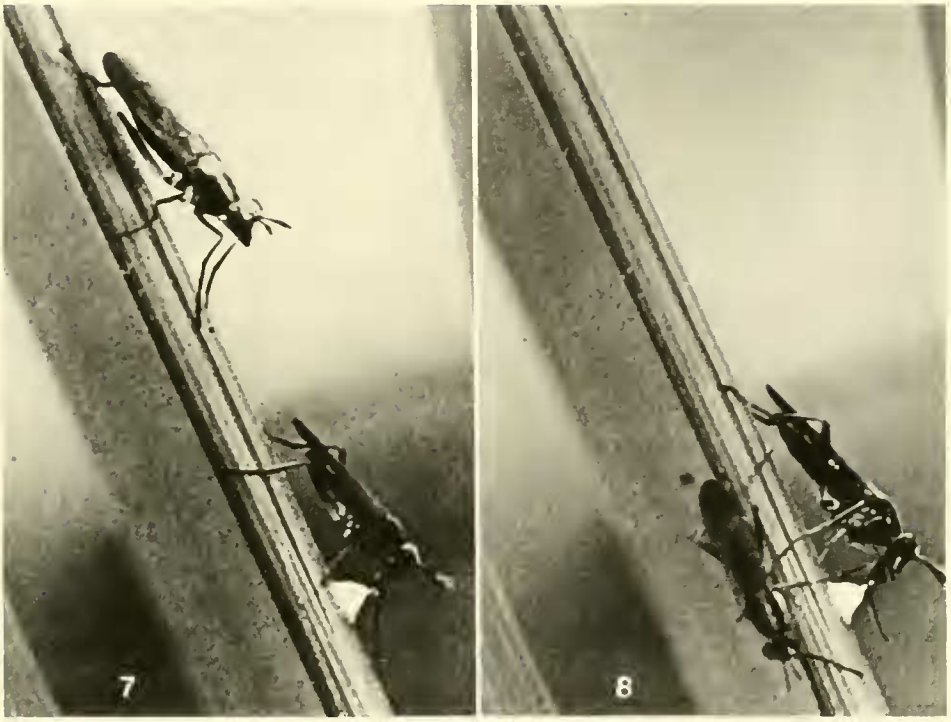
The other mating female clearly was not eating. There was no white, frothy material near her, and she did not extend her labellum to the substrate during the 12 minutes she was observed in copula.

A courtship and mating act observed two days later convinced us that the nuptial food of this species also is secreted from the tip of the male's abdomen. A fly was holding the end of its abdomen on the substrate in a posture suggesting oviposition. However, this individual was a male, and the substance being deposited was a low, flat droplet only about half the diameter of the fly's head. He lifted the tip of his abdomen two or three times and touched it down again, as if to deposit more of this transparent, faintly whitish fluid.

A minute later, he turned and began to work this material with his labellum. The mass quickly became much more conspicuous—larger in diameter and in height and opaque white instead of almost completely clear and colorless. A female fly approached, stopped about 3 cm from the mass, and stood still, evidently watching (cf. Fig. 7).

After about three minutes, the female walked forward (cf. Fig. 8). The male leaned away from her, as if to get out of her way so she could make contact with the white mass. As soon as she did he stepped up onto her, and they copulated almost immediately.

When her tarsi apparently slipped, the mating pair fell to the moss covering the bottom of the observation cell. She walked, carrying the male, back up the vertical wall of the cell (about 4 cm), found the white mass about a minute later,



Figs. 7, 8. A male of *S. aenescens* whips the nuptial food into an opaque, white froth and attracts a female to it. (Both from S.-Y. Lee, in Green, 1977).

and resumed feeding. Sexual contact apparently was not broken during this episode.

A male fly approached the mating pair and fed on the white mass with the mating female. Then he stepped up onto the mating pair and apparently tried to copulate with the copulating male. The white mass was now reduced to about half the size of a fly's head. The second male again joined the female in feeding on it. About five minutes after his first approach, he tried again to mate with the mounted male, then walked away.

About 12 minutes after the female started to feed and mating began, we could no longer see any nuptial food. However, continued labellar action of the female indicated that she tried for two more minutes to get more food. The pair then sat still, but we observed five minutes later that they were no longer in copula, and a minute after that (18 minutes after copulation began) the male dismounted.

Observations of the mating of *S. aenescens* show great variability in nuptial feeding. We have seen just as many mating pairs in which the female clearly was not eating anything as pairs in which female feeding was involved. The behavior lacks uniformity and predictability also because the male frequently eats the secreted nuptial food himself. This sometimes happens after a male has whipped it into a frothy mass and tried to attract a female, but males also have been observed to deposit the clear liquid anally, then promptly turn and eat it.

We have not observed males of either *S. aenescens* or *S. f. floridensis* using other foods (e.g. dead snails) to attract receptive females. However, we have spent less time watching those species and we were not specifically looking for it. *Sepedon f. fuscipennis* almost certainly is not the only taxon of *Sepedon* utilizing this mating system; a slide showing the female of *S. sphegea* (Fabricius) (Palearctic) feeding on a dead snail during copulation suggests that it may be used in that species.

Observations of Others on Asiatic Species of *Sepedon*

Observations of courtship and mating of *Sepedon* have been made by others on four palearctic species. Sung-Yang Lee (in Green, 1977) observed and photographed a "sciomyzid fly" on Taiwan that he did not further identify. His excellent color pictures (reproduced here in black and white as Figs. 7 and 8) identify the subject positively to the genus *Sepedon* and suggest strongly that it is *S. aenescens*. Ookeow Beaver (unpublished) observed courtship and mating of *S. senex* Wiedemann and *S. plumbella* Wiedemann in Thailand, and K. Durga Prasad (presumably unpublished) observed these activities of *S. aenescens*, *S. plumbella*, and *S. ferruginosa* Wiedemann in India.

Those observations were made several years ago, and further publication of them now appears unlikely. However, observations of such significance should be recorded and preserved. By differing from ours in fundamental ways, they pose important questions that should be raised. We are therefore taking the liberty of summarizing the observations of Mr. Prasad and Dr. Beaver and of quoting excerpts from the research notes they kindly sent us.

Lee reported that the male of what appears to be *S. aenescens* exudes a white, frothy substance orally and that this material is eaten by the female during copulation (Figs. 7, 8). Prasad corroborated this in observations recorded under *Sepedon sauteri* Hendel, a junior synonym of *S. aenescens* (Knutson and Orth, 1984). He added that he has "many times" observed production of the "white mass" in nature, with several female flies and "sometimes even male flies" congregating within a radius of 15 cm "in an excited condition."

In a section entitled, "Origin of the White Mass," Prasad recounted the dissection of flies of both sexes without identifying the species involved. He found "long, coiled salivary glands reaching almost the tip of the abdomen" in males. In females, those glands were "much shorter, smaller in diameter," and only "half the size" of the male salivary glands. He concluded that the male salivary glands enlarged as they assumed the added function of producing the nuptial food.

Beaver first saw the "viscous, white material" on the mouthparts of a male *S. senex*. She watched him place it on the substrate, saw mating occur as the female consumed it, then saw that "more of the substance oozed out from his proboscis." Although we had told her of our conviction that *S. aenescens* produces the nuptial food anally, she remains convinced, after watching this and several other matings of *S. senex*, that this species produces it orally.

Both Prasad and Beaver reported production of the "white mass" as an important element in the mating behavior of *S. plumbella*. Prasad stated that it is secreted "through its labellum," and Beaver's wording is "from his proboscis." Prasad indicated that the male "guards it aggressively by lifting its forelegs and swiping at the incoming female." Both recounted "pseudofights" between the

male and female, a term[1] that Beaver applied also to premating activities of *S. senex*.

Both stated that males of *S. plumbella* produced more white material while mating. This is another phenomenon that Beaver also observed in *S. senex* and another indication of great similarity in the courtship and mating activities of these two species. Prasad mentioned watching a male *S. plumbella* produce the "white mass" five times in about 15 minutes, finally attracting a female and mating with her. While still mounted, it produced a sixth issue of nuptial food, finally dismounting with "a big white mass sticking to its labellum." It placed this material on a leaf, manipulated it with its mouthparts until the female was attracted again, and mated again.

In *S. ferruginosa*, Prasad believes that nuptial food functions more to pacify females during copulation than as a lure to get them to mate.[2] Although males of that species sometimes produce this material before mating and use it to attract the female, he saw several matings that started without any evidence of nuptial food. The males simply jumped onto the females.

However, he saw much evidence of its production after mating was in progress, with males producing it one, two, or three times during a mating process. These males produced the white material orally, and it came out "in the form of coils." They placed it on the antennae of their female partners, and some females removed it with their forelegs and devoured it while mating. Others removed it, but left it on the substrate in front of them. In such instances, the male usually ate this material after he dismounted.

Discussion

Extent of Nuptial Feeding in Sciomyzidae and Other Diptera.—Nuptial feeding is known in the dipterous families Empididae (Downes, 1970, and references therein), Micropezidae (Wheeler, 1924), Platystomatidae (McAlpine, 1973, and papers cited therein), Sciomyzidae (Green, 1977, and this paper), Tephritidae (reviewed by Friedberg, 1982), and Asteidae (Friedberg, 1984).[3]

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[1] This term evidently refers to the state of strife when a female tries to feed without signalling her willingness to mate, and the male seems determined to prevent this. Probably because it is followed quickly in many instances by the ultimate gesture of amiability, Beaver and Prasad evidently concluded that it is not a real fight. However, males that defend a rich food resource in order to attract mating partners assault all intruders except *receptive* females with surprising vigor. Until a female signals her receptivity, she is, like other intruders, just stealing the male's valuable resources and giving nothing in return.

[2] Neither he nor Beaver mentioned its possible value in nourishing the female for greater egg production.

[3] Consideration of the foods and feeding habits of these flies raises serious doubts concerning the proposition of Kessel (1955, p. 98) and others, that nuptial feeding serves to protect the lives of courting males from predatory and potentially cannibalistic females. Only the Empididae and the Micropezidae are predatory, and the Micropezidae prey only on much smaller insects. Thus, lives of the males are in no jeopardy in five of the six families. Even in the Empididae, where cannibalism of males by females is known to occur, closer observation has indicated that the males thus victimized probably were newly emerged and teneral. Downes (1970, p. 790) wrote that he could not "find any record in the literature of the eating of the male by the female *at the time of mating* (our italics) either in the three genera in question or in other Empididae." In the robber flies (Asilidae), where the

In the Sciomyzidae, there are indications that nuptial feeding is widespread not only in species of *Sepedon*, but also in two closely related genera. *Sepedomerus* was split off from *Sepedon* (Steyskal, 1973) to receive Neotropical species having relatively minor differences from the taxa retained in *Sepedon*. The Neotropical genus *Thecomyia* is not quite so close to *Sepedon*, yet far more similar to it than are most genera of the Tetanocerini. Steyskal (1973) placed it in the "*Sepedon* group," a distinctive assemblage of genera that Steyskal and Verbeke (1956) had earlier called the Sepedoninae.

Neff and Berg (1966) were reporting observations made primarily on *Sepedomerus caeruleus* (Melander) when they wrote: "Prior to mating, the male . . . forelegs are raised and lowered nervously and a bobbing motion of the abdomen occurs. His wings are extended laterally from their resting position over the abdomen, vibrated rapidly for several seconds, and then returned to the resting position. The frequency of these wing vibrations increases as long as the female remains still and presumably receptive; however, if she backs away and flicks her wings several times in quick scissors-like movements, the male ceases his display. If the female remains still and gives no wing motion, the male circles behind her slowly and mounts her from behind."

Concerning *Thecomyia limbata* (Wiedemann), Abercrombie and Berg (1975) wrote: "Prior to mating, the male frequently stands about 5–7 cm in front of the female, waving his forelegs while resting on his mid- and hindlegs. At the same time, he holds his wings obliquely upward and outspread."

Although neither quotation mentions the inconspicuous droplet of nuptial food, and the latter does not even stipulate that the male's outstretched wings were vibrating, a detailed reexamination of courtship probably would reveal that nuptial feeding is involved in both species. It is far more significant that certain male actions associated only with the sciomyzid species known to employ nuptial feeding were observed than that other actions associated with those males were not. We often fail to see what we are not looking for, even when it is clearly visible.

An Oral or Anal Secretion?—The contrasting observations of courtship and mating reported here suggest fundamental differences that are not easily explained. Before we saw the research notes of Beaver and Prasad, we felt comfortable with the conclusion that *Sepedon* males secrete the nuptial food anally. This is unquestionably true in *S. f. fuscipennis* and *S. f. floridensis*, where male mouthparts never contact this material unless the male decides to eat it.

Opinions that it is secreted orally seemed accountable to incomplete observations of courtship in *S. aenescens*. The small, clear droplets secreted anally by males of that species are not easily seen, and Lee (in Green, 1977) presumably never looked for them. He probably did not suspect that premating activity had begun until after the male turned and got his labellum into this material. Therefore, he drew the logical but erroneous conclusion, "To woo his chosen mate, this six-legged lover exudes a white froth from his mouth . . . ."

However, we cannot conclude that Beaver and Prasad were overlooking an anal origin of nuptial food when they saw it appear on the mouthparts of males that

assertion that nuptial feeding protects the lives of courting males (Cloudsley-Thompson, 1961, p. 89) may seem completely credible, female feeding while *in copula* evidently does not result from nuptial feeding, but from opportunistic males pouncing on females with prey! Dennis and Lavigne (1975, p. 49) stated, "There is no evidence to suggest that males offer females food . . . ."

were already in copula. Since copulating males could not turn to recover an anally secreted substance, oral secretion seems evident in the three species concerned, *Sepedon senex*, *S. plumbella*, and *S. ferruginosa*.

It may seem unlikely that closely related species are producing this material in totally different parts of their bodies. However, Alcock (1981) has reported both oral and anal secretion of nuptial food in closely related species of Australian thynnine wasps. Perhaps the course of evolution of nuptial feeding in *Sepedon* may suggest an explanation of this puzzling situation.

The Evolution of Nuptial Feeding in *Sepedon*.—The ability of *Sepedon* males to secrete a nuptial food probably evolved by a gradual, step-wise process. As indicated above, males of *S. f. fuscipennis* often take possession of food items that they have found, defend them against other flies, and use them both to attract a willing female and to occupy her attention during a prolonged mating process. When they find dead snails that have dried and formed hard surface crusts, they deposit droplets of the nuptial food on them, soften the crust, and render them accessible for hungry females.

This suggests that the first step in the evolution of nuptial food deposit may have been the habit of placing a droplet of liquid from the hind gut onto any dried animal matter found in nature. Males secreting this liquid would have had positive selective advantages, even if it contained no nutritive substances nor volatile pheromones. By simply moistening bits of dried animal matter, they made them valuable to the females as food, hence valuable to themselves as female attractants.

Pheromones and other additives may have evolved later in some species of *Sepedon*, either incorporated into the nuptial food or released in association with it. Courting males of several insect species combine nuptial feeding with pheromone production, and the *Sepedon* habit of rapidly vibrating their wings after depositing this material suggests a pheromone-dispersing function. Pheromone dispersal is the demonstrated or suggested function of rapid wing vibrations following the eversion of abdominal glands and/or the extrusion of visible droplets by courting males of a drosophilid and two tephritids (Spieth, 1974, p. 397; Féron, 1962, p. 37–45; Friedberg, 1982).

However, the "nuptial food" deposited anally may still be nothing more than hind gut contents. When the male of *S. aenescens* turns and whips the anal secretion into an opaque froth, he may be adding salivary secretions to supply nutrients, pheromones, and substances to partially solidify this material. This would suggest why the male salivary glands may be enlarged even in a species that begins by depositing a droplet anally. It might also suggest an evolutionary link between a primitive practice of simply moistening existing food with a droplet of gut contents and an advanced condition of relying solely on the salivary glands to supply semi-solid, and perhaps nutritious and pheromone-impregnated nuptial food.

Conclusions and Suggestions for Future Research

Males of *Sepedon f. fuscipennis* that find a freshly killed snail[4] advertise its availability to potential mates by conspicuous movements of their wings, abdo-

[4] *Sepedon* larvae are voracious snail predators that abandon their prey when satiated. Since the weak-flying adults remain in larval breeding sites, snails killed by their larvae may be their major

mens, and forelegs. Males of this and other species of *Sepedon* also attract receptive females by similar displays after releasing oral and anal secretions. These probably consist chiefly of snail tissues digested and transformed to varying degrees. *Sepedon* males that do not offer their potential mates either secretions or a snail often jump onto females and sometimes succeed in mating.

Like males of other species that can monopolize a rich food resource, *Sepedon* males that either "possess" a snail or release secreted nuptial food have something of value to offer to receptive females. They may therefore have unusual reproductive success relative to other males in their populations. Mating systems in which males find and defend resources to which females will be attracted (oviposition sites as well as foods) are discussed informatively by Thornhill and Alcock (1983, p. 248–252).

Our objectives in publishing this preliminary report are to stimulate someone to make a far more thorough study of this intriguing subject, to lay some groundwork for launching that study, and to suggest some profitable avenues of investigation. Unanswered questions that merit further research are suggested or implied throughout. Other questions very worthy of study are suggested by the striking degree of convergence between *Sepedon* and *Panorpa* (Mecoptera: Panorpidae) (Thornhill, 1981; Thornhill and Alcock, 1983, p. 271–272). The three alternative techniques utilized by males of *Panorpa* to obtain a mating closely resemble the three listed above for males of *Sepedon*.

In some species of *Panorpa*, males defend rich food resources (e.g. dead crickets) and enjoy disproportionate reproductive success. Others, if sufficiently well fed, offer salivary masses to females, who will accept them if there are no carrion defenders at the site. Still others, less well fed, attempt to mate without offering females anything. Sometimes, although rarely, they succeed in doing so.

Would a quantitative study of *Sepedon* and related genera reveal that the reproductive success of males is proportional to the resources they control, with males on freshly killed snails doing better than secretion producers, which in turn do better than those without a gift? Would it also show that female fecundity and the interval between this and the next mating are proportional (as in *Panorpa*) to the food ingested during each mating? In short, does the male that offers a nuptial gift gain the advantage that his mate will lay more eggs fertilized by him than by a male that cannot offer anything?

Acknowledgments

Ookeow Beaver, Department of Biology, Chiangmai University, Chiangmai, Thailand, and K. Durga Prasad, then a biology student at the College of Agriculture, Hebbal, Bangalore, India, kindly sent us their unpublished research notes, then corresponded repeatedly with us to try to explain the contrasts between their observations and ours. Sung-Yang Lee, entomologist and expert insect photographer of Taiwan, made the photographs reproduced here as Figs. 7 and 8. David Grimaldi made the drawings (Figs. 1–6) and counselled with us concerning the manuscript and pertinent literature. R. E. Orth checked our voucher specimens

source of protein (Berg and Knutson, 1978, p. 246). The importance of this rich food resource is now seen to extend beyond their own nourishment to play crucial roles in reproductive success of the males and in essential nourishment that the females translate into egg production.

of *S. f. fuscipennis* and *S. f. floridensis*, confirmed our identifications, and returned this material for deposit in the Cornell University Insect Collection. He and B. A. Foote, L. Knutson, and S. E. Neff read and suggested improvements in the manuscript. We are especially grateful to John Alcock, whose special interest in insect mating systems and broad knowledge of them made his comments uniquely valuable.

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